

Ultraviolet-B radiation: a potent regulator of flavonoids biosynthesis, accumulation and functions in plants

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Flavonoids represent a diverse group of polyphenolic secondary metabolites which are distributed amongst most of the plant species. Ultraviolet-B (UV-B) radiation is one of the important environmental regulators which governs the flavonoids biosynthesis at the transcriptional level. It is important to find out the role played by UV-B radiation in regulation of flavonoids biosynthesis and function under UV-B stress conditions in plants. This article summarizes the existing knowledge on the regulatory role of UV-B radiation on flavonoids biosynthesis and its accumulation trends in plants; further it discusses the diverse functions of flavonoids under the influence of UV-B radiation in plants.

Keywords: Flavonoids, plant species, potent regulator, reactive oxygen species, ultraviolet-B radiation.

ULTRAVIOLET (UV) radiation of the solar spectrum has been divided into UV-A (315–400 nm), UV-B (280–315 nm) and UV-C (less than 280 nm), of which UV-B part of the spectrum is of great biological importance. Stratospheric ozone (O₃) depletion as a result of anthropogenic production of O₃-depleting substances is the conventional cause of enhanced UV-B radiation on the Earth's surface, whereas more recently studied causes as the O₃ layer recovery occurs are aerosols, cloud cover, greenhouse gases and hydrofluorocarbons¹. Since terrestrial plants are immovable and unavoidably exposed to high-energy radiation, this influences the plants by directly damaging macromolecules, generating reactive oxygen species (ROS) and impairing various cellular processes^{2,3}. Plants have therefore evolved various defence-related processes to overcome UV-B radiation generated oxidative stress. One such defence strategy is the production of higher amounts of flavonoids. These are a diverse group of secondary metabolites, estimated to be over 10,000 (ref. 4), which are found in most plant tissues. The basic skeleton of a flavonoid contains 15 carbons that are confined in two aromatic rings (A and B) connected by a heterocyclic pyran ring (C), and are classified into several

groups on the basis of degree of oxidation and saturation of the heterocyclic ring⁵. The basic carbon skeleton of the flavonoids may have several substituents; sugars are common. In general most of the flavonoids are found naturally as glycosides⁶. Due to their diverse chemical structure and variety, different types of flavonoids perform specific functions in plants. Flavonoids are present generally in the uppermost epidermal cells of leaves as well as in trichomes, glandular hair and mesophyll cells^{7,8}, flavonoids also accumulate intracellularly in different cell organelles such as, vacuoles, chloroplasts and nucleus^{9–11}. Flavonoids protect plants by absorbing harmful UV-B radiation, scavenging ROS formed due to imposed stress and preventing oxidation of biomolecules^{11,12}. The first direct evidence related to protecting role of flavonoids against UV-B radiation came from *Arabidopsis*, *transparent testa (tt)* mutant, which had less content of flavonoids and highly sensitive to UV-B radiation as compared to its wild-type when grown in the influence of high UV-B radiation¹³. Since flavonoids impart protection against UV-B radiation, their biosynthesis is also regulated by UV-B radiation which leads to accumulation of flavonoids in UV-B radiation-sensitive tissues. To date, several enthralling studies have been done at molecular level to find the role of UV-B radiation in biosynthesis and accumulation patterns of flavonoids in several models, crops and fruit-bearing plant species, but relatively a handful studies have focused on wild and medicinally important plants as they are also a good source of flavonoids and proved to be important for lives. This article summarizes several aspects of flavonoids biosynthesis at molecular level under the influence of UV-B radiation in models, crops, legumes, fruits bearing plants, grasses, wild and medicinal plants, and also focuses on flavonoids accumulation and functions in general, in response to UV-B radiation.

Review

Literature search

A literature review was carried out through searching peer-reviewed articles on the internet and in the libraries,

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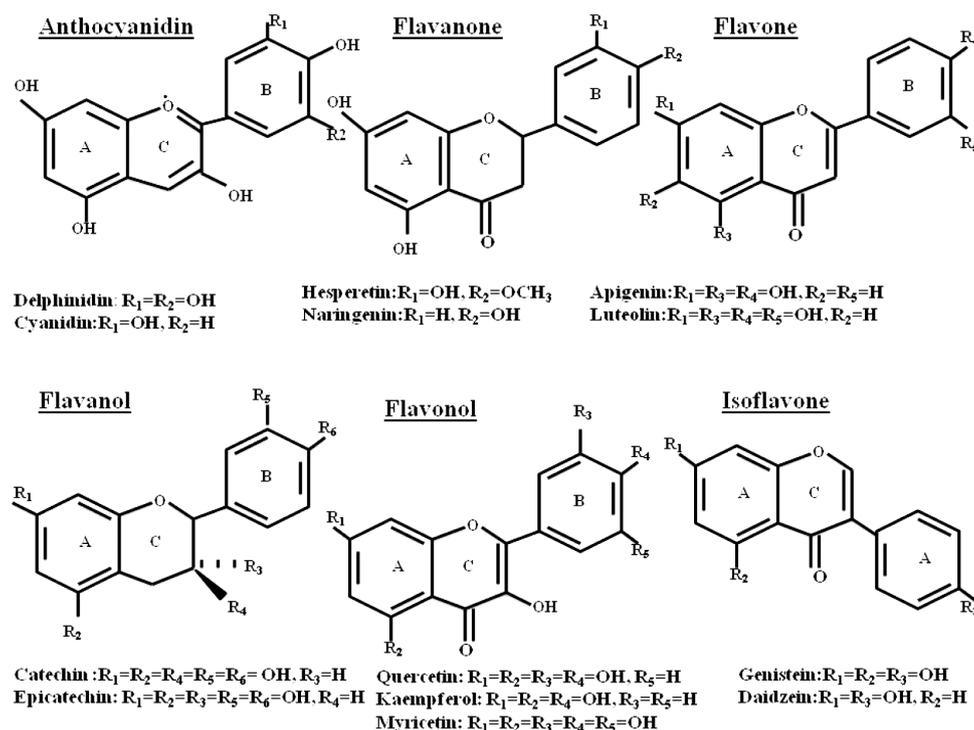


Figure 1. Diagrammatic representation of different classes of flavonoids with representatives of each class (modified from Dai and Mumper⁹⁹).

published over a period of 25 years (1993–2018). The literature search was performed through search databases such as Google Scholar, Pubmed, ScienceDirect, ResearchGate, Springer, Elsevier using several keyword combinations and search terms (e.g. flavonoids biosynthesis, UV-B regulation, flavonoids function, UV-B and flavonoids, UV-B signal transduction, etc). Further, we reviewed all selected abstracts that met the inclusion criteria: articles with keywords in the title, abstracts and full text. From the initial search 205 papers were selected and after screening 78 papers which were related with UV-B radiation exposure, and flavonoids biosynthesis and accumulation were further explored.

Biosynthesis of flavonoids

Flavonoids represent the largest class of polyphenols. Generally, they are classified into various families of 15 carbon containing molecules such as flavones, flavonols, flavanones, flavanols, anthocyanidins and isoflavonoids¹⁴. Figure 1 shows the structure of different classes of flavonoids, with a representative of each class. Flavonoids are synthesized as the branch of phenylpropanoid pathway⁵. The key precursor of the general phenylpropanoid pathway is phenylalanine, which is deaminated by the action of an important enzyme phenylalanine ammonia-lyase (PAL) to cinnamic acid. Further cinnamic acid undergoes hydroxylation reaction and converted into p-coumaric acid by the action of cinnamic acid 4-hydroxylase (C4H). The carboxylic group present in

p-coumaric acid is activated to form p-coumaroyl-coenzyme A (CoA), this process is catalysed by p-coumaroyl CoA ligase (4CL)¹⁵. Then the p-coumaroyl-CoA (1 molecule) and malonyl CoA (3 molecule) react to form chalcone by the involvement of an enzyme chalcone synthase (CHS), an enzyme which is specific for flavonoids biosynthesis pathway and catalyses the production of chalcone scaffold, from which all flavonoids are derived¹⁴. The formation of flavanone from chalcone then occurs through isomerization performed by chalcone isomerase (CHI). The biosynthesis pathway branches to various other classes of flavonoids. Figure 2 shows the biosynthesis pathway leading to different flavonoid classes. However, the principal pathway for the biosynthesis of flavonoids is conserved in plants; depending on plants a number of enzymes modified the basic skeleton of flavonoids and lead to formation of different classes of flavonoids¹⁶.

UV-B radiation mediated signalling pathway of flavonoids biosynthesis

Flavonoids biosynthesis and its accumulation are both developmentally and environmentally controlled in plants^{17,18}. UV-B radiation is an environmental stimulus which regulates flavonoids biosynthesis⁶. Plants perceive this radiation through a specific UV-B receptor, viz. UVR8 (ref. 19) and several other components, that takes part in the downstream signalling pathway^{20,21}. From UV-B radiation perception to downstream signal transduction

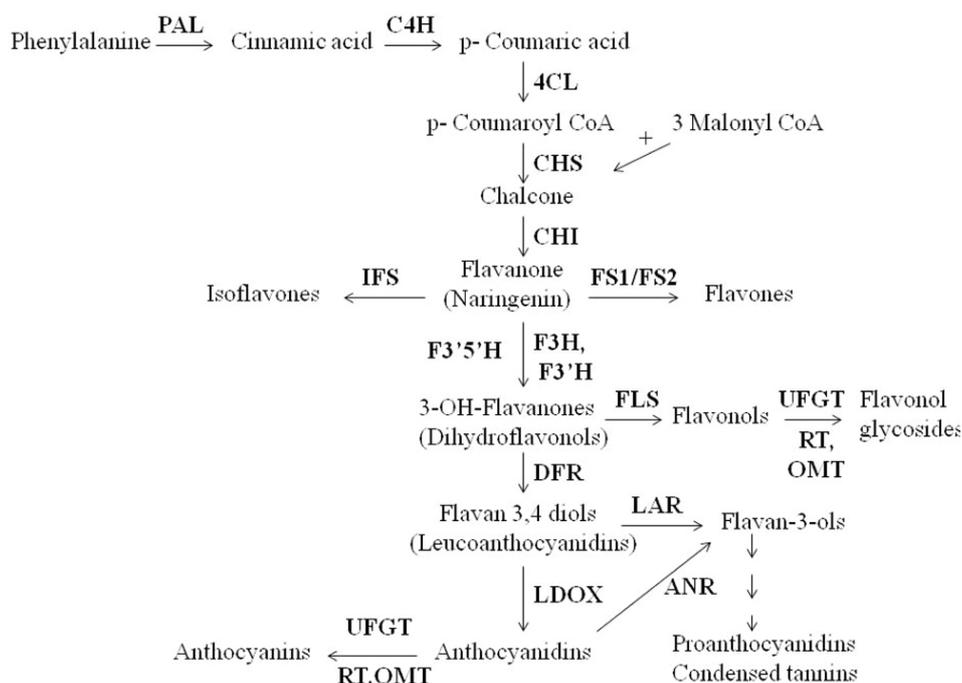


Figure 2. Schematic representation of flavonoids biosynthetic pathway (modified from Winkel-Shirley⁵¹). PAL, Phenylalanine ammonia-lyase; C4H, Cinnamate-4-hydroxylase; 4CL, 4-Coumarate-coA-ligase; CHS, Chalcone synthase; CHI, Chalcone isomerase; IFS, Isoflavone synthase; FS1/FS2, Flavone synthase; F3H, Flavanone 3-hydroxylase; F3'H, Flavonoid 3' hydroxylase; F3'5'H, Flavonoid 3'5' hydroxylase; FLS, Flavonol synthase; DFR, Dihydroflavonol reductase; LAR, Leucoanthocyanidin reductase; LDOX, Leucoanthocyanidin dioxygenase; ANR, Anthocyanidin reductase; UFGT, UDP flavonoid glucosyl transferase; OMT, O-methyltransferase; RT, Rhamnosyl transferase.

pathway, flavonoids biosynthesis is highly conserved between the earliest land plant, a liverwort (*Marchantia polymorpha*) and highly evolved flowering plants like *Arabidopsis thaliana*²². The UVR8 photoreceptor occurs as a homodimer in cytosol which passes through rapid monomerization on exposure of UV-B radiation mediated by tryptophan residues that serve as UV-B chromophore²³. Activated UVR8 monomer then interacts with COP1 (a multifunctional E3 ubiquitin ligase)²⁴. In addition, UVR8 monomers is redimerized through a negative feedback loop via REPRESSOR OF UV-B PHOTOMORPHOGENESIS (RUP1) and RUP2 (a WD40-repeat proteins), which inactivate the pathway by interrupting the interaction of UVR8-COP1 and regenerate again homodimer of UVR8 (ref. 21). COP1 plays an important role in the nuclear accumulation of UVR8, initiate the molecular signalling pathway²⁵. By promoting degradation of HY5 (ELONGATED HYPOCOTYL 5, which is a bZIP transcription factor) COP1 alone represses photomorphogenesis in plants, but following interaction of COP1 under UV-B radiation with the UVR8 monomer, HY5 is prevented from COP1-mediated degradation^{24,26}. Thus, the UVR8–COP1 complex stabilizes HY5 and, in turn, HY5 and HYH (HY5 HOMOLOG) promote the activity of various R2R3MYB transcription factors for the transcription of genes required in flavonoids biosynthesis pathway^{17,23,27}. Figure 3 summarizes the process of UV-B radiation-mediated signal transduction pathway of flavonoids biosynthesis in plants. In *A. thaliana*, HY5 regulates

the expression of *AtMYB12* in response to UV-B radiation²⁸. Recently, Yang *et al.*²⁹ also reported that in *Chrysanthemum morifolium* CmUVR8, COP1 and HY5 played a prominent role in UV-B radiation-induced expression of the genes of the flavonoids biosynthesis pathway, which resulted in the accumulation of several classes of flavonoids.

UV-B radiation: a potent regulator of genes of the flavonoids biosynthesis pathway

UV-B radiation regulates flavonoids biosynthesis at the transcriptional level of the gene that encodes corresponding enzymes of the biosynthetic pathway³⁰. In addition, these genes are controlled by a key transcription factor R2R3MYB, one of the four major MYB group transcription factors³¹, in several plant species^{17,32,33}. This regulation occurs through particular binding of transcription factors to motifs present in promoter region of the biosynthetic pathway genes³⁴. The R2R3MYB transcription factors coordinately regulate the structural genes of the flavonoids biosynthesis pathway by activating or repressing their expression. In *Arabidopsis*, several genes such as *CHS*, *CHI*, *F3H* and *FLS1* participated in early biosynthesis steps are transcriptionally regulated by three closely related R2R3MYB transcription factors, viz. MYB11, MYB12 and MYB111. The late flavonoids biosynthesis pathway genes are also regulated by MBW complex (ternary transcriptional complex) consisting of

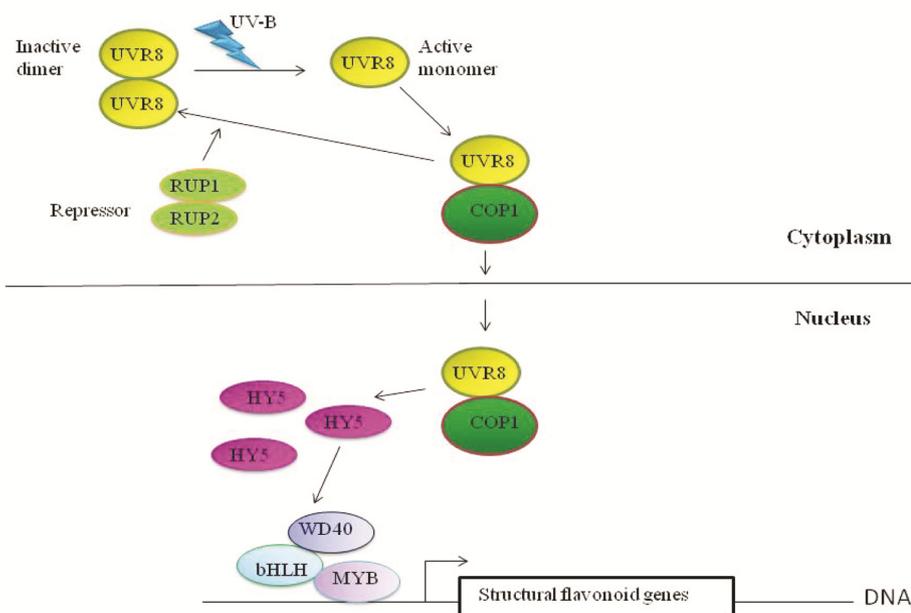


Figure 3. Diagrammatic representation of UVR8-mediated signal transduction pathway of flavonoids biosynthesis (modified from Zoratti *et al.*²⁷). UVR8, A UV-B receptor; COP1, CONSTITUTIVELY PHOTOMORPHOGENIC 1; HY5, ELONGATED HYPOCOTYL 5; MYB transcription factor, V-myb myeloblastosis viral oncogene homolog; bHLH, Basic helix–loop–helix; WDR, Tryptophan–aspartic acid repeat and RUP1/2, REPRESSOR OF ULTRAVIOLET-B PHOTOMORPHOGENESIS.

R2R3MYB, basic helix–loop–helix (bHLH), and tryptophan–aspartic acid repeat (WDR)³⁵. A study by Morales *et al.*³⁶ on *Betula pendula* (birch) leaves, it was found that *PAL* and *HYH* transcripts decreased linearly when UV-B radiation was excluded, indicating that expression of these genes were regulated at the transcript level by radiation in birch leaves. Under UV-B radiation, overexpression of *MYB134*, a R2R3MYB transcription factor gene in *Populus* species, resulted in transcriptional activation of the proanthocyanidin (a flavonoid class) pathway and an increase in proanthocyanidin level³⁷. Liu *et al.*³⁸ found that in *Vitis vinifera*, a R2R3MYB transcription factor gene *VvMYB12* was responsive to UV-B radiation and *VvFLS4* gene also showed induced expression under exposure to the radiation. In *Pinus taeda*, it has been hypothesized that PtMYB1 binds to the promoter region of *PAL* gene and activates its transcription³⁹. UV-B radiation exposure induces *ZmFLS1*, an *Arabidopsis* (*AtFLS1*) homologue in *Zea mays* via increased expression of MYB/bHLH transcription factors P1, B and PL1 (ref. 40). In *Reaumuria soongorica* UV-B radiation also induces expression of *RsF3H* gene and the activity of enzymes leading to an increase in the content of total flavonoids and anthocyanins⁴¹. Recently, Pandey *et al.*⁴² reported that enhancement in the expression of *AaPAL1* gene in a medicinal plant *Artemisia annua*, resulted in enhanced flavonoids biosynthesis upon exposure to UV-B radiation. Gotto *et al.*⁴³ found that UV-B radiation supplementation to *Lactuca sativa* plants induced the expression of *CHS* and *UFGT*, leading to an increased concentration of anthocyanin. Casati and Walbot⁴⁴ reported *Z. mays* from high altitude responded to UV-B radiation

by accumulation of maysin and rhamnosylisoorientin flavones and the accumulation of these flavones in leaves was controlled by expression of a p-homologous transcription factor which is further regulated by UV-B radiation. In *Vaccinium corymbosum* cv. Brigitta and Bluegold, UV-B radiation significantly induced transcription factor gene *VcMYBP1* in both genotypes. This could be key for the synthesis of anthocyanin due to activation of structural gene of the biosynthesis pathway⁴⁵. Huang *et al.*⁴⁶ revealed that UV-B radiation effectively elicits and changed the abundance of *FtPAL*, *FtCHS*, *FtCHI*, *FtF3H* and *FtFLS-1* transcripts in hairy root culture of *Fagopyrum tataricum*. Park *et al.*⁴⁷ found that accumulation of anthocyanins was correlated with the activities of *CHS*, *F3H* and *DFR* genes of the biosynthesis pathway in lettuce leaves irradiated with UV-B radiation. Exposure of UV-B radiation and white light have been shown to enhance the expression of *MYB10* and *bHLH3* transcription factor genes, leading to an enhancement in expression of *UFGT* and accumulation of anthocyanins in *Prunus persica* cv. Stark Red Gold⁴⁸. *Reaumaria trigyna* plants showed increased expression of *RtMYBF1* transcription factor gene, which was associated with an increased expression of flavonoids structural genes *RtC4H*, *RtF3'H*, *RtFLS1*, *RtFLS2*, *RtF3'5'H*, *RtOMT* after exposure, leading to stimulation in the flavonols level⁴⁹.

Flavonoids accumulation in plants under the influence of UV-B radiation

Flavonoids accumulation is a common or universal response to UV-B radiation and has been directly related to

UV-B radiation absorbing nature of flavonoids⁵⁰. Among the flavonoids, flavonols represent the ancient and widespread class of flavonoids and are synthesized even in the lower plants such as in mosses and ferns⁵¹. Multiple hydroxyl group containing flavonoids have better ROS scavenging activity⁵², and several studies have reported that under UV-B radiation ortho-dihydroxy B-ring-substituted flavonoids (quercetin and luteolin) disproportionately increase in comparison to monohydroxy B-ring-substituted (kaempferol and apigenin) flavonoids and inhibit the generation of ROS, and thus functioning as an antioxidant^{11,50}. Smith and Markham⁵³ suggested that quercetin glycoside better dissipate UV-B radiation through keto-enol tautomerization than the equivalent kaempferol glycosides. UV-B radiation also induces differential accumulation of orthodihydroxylated flavonoids than monohydroxylated flavonoids that have also been observed for two cultivars, viz. *Oryza sativa*⁵⁴ and *Brassica napus*⁵⁵. Hofmann *et al.*⁵⁶ reported that higher ratio of quercetin to kaempferol due to UV-B radiation was conserved for a genetically diverse population of *Trifolium repens*. Takshak and Agrawal⁵⁷ reported that increased activities of PAL, 4CL, CHI, CAD and DFR directly corresponds to enhanced level of anthocyanins, flavonoids and tannins in a medicinal plant *Withania somnifera* under supplemental UV-B radiation ($3.6 \text{ kJm}^{-2}\text{d}^{-1}$). In the grass and sedge species *Deschampsia antarctica*, *D. borealis* and *Carex arenaria*, high levels of constitutive flavonoids were found, which protect them against the elevated levels of solar UV-B radiation⁵⁸. Chaudhary and Agrawal⁵⁹ observed a higher concentration of quercetin at the initial age under UV-B in two cultivars of *Vigna radiata*, which might have provided additional protection against UV-B radiation at the initial stage of plant growth. In *Cymbopogon citratus*, flavonoids content increased by 53% at a higher dose of UV-B radiation ($3.6 \text{ kJm}^{-2}\text{d}^{-1}$) and was positively correlated with PAL activity⁶⁰. In the natural environment, plants are generally exposed to several stresses simultaneously. Studies have also reported accumulation of flavonoids in plants by several environmental factors in addition to UV-B radiation. Reuber *et al.*⁶¹ reported that UV-B radiation and low PAR light stimulate the activity of chalcone synthase (CHS), which was directly correlated with flavonoids in leaf tissues of *Secale cereale*. In *Ligustrum vulgare*, quercetin 3-O- and luteolin 7-O-glycosides were found to be accumulated against salinity and UV-B radiation stress⁶². UV-B radiation (0.90 Wm^{-2}) and PAR light of higher intensity ($1350 \mu\text{mol m}^{-2}\text{s}^{-1}$) leads to different kind of responses in white and green variegated leaves of *Pelargonium zonale*, which represents a model system for studying source-sink interactions within the same leaf. PAR light of high intensity had major influence on the green sector of the leaves and induce flavonoids having antioxidative function whereas UV-B radiation had a major influence on white leaf sector and induce flavonoids accumulation with UV-B radiation screening

function. In addition, UV-B radiation compensates the lack of photosynthetic activity and biosynthesis of flavonoids in white tissue by stimulating allocation of C from green (source) tissues to white (sink) tissues⁶³. In another variegated plant, *Plectranthus coleoides* the same dose of UV-B and PAR as above induced three-fold increase of apigenin glycoside in both white and green tissues, and the greatest amount was found in UV-B and low PAR intensity⁶⁴. In general, effect of an elicitor on the secondary metabolites content in a plant species rely on elicitation intensity and time of exposure. According to Jiao *et al.*⁶⁵, UV-B radiation of high intensity could cause damage to various cellular macromolecules such as lipids, proteins and nucleic acids. Jiao *et al.*⁶⁵ revealed that mild doses of UV-B were more appropriate for stimulation of isoflavonoids in *Astragalus membranaceus* hairy root culture. In *Ocimum basilicum*, intermittent dose of 3.60 Wm^{-2} was found to increase the levels of flavonoids and improvement in medicinal quality of the plants⁶⁶. Table 1 summarizes the impact of UV-B radiation dose and time of exposure on the accumulation of different classes of flavonoids in different plants species.

Thus a clear picture emerges indicating a highly specific pattern of flavonoids accumulation in plants in response to UV-B, which is further affected by various other regulatory factors such as intensity of radiation, time of exposure, developmental stage of plants, genetic setup of species and cultivars, chemical structure of flavonoids as well as presence of other environmental factors^{46,49,64,67,68}.

Functions of flavonoids in plants under the influence of UV-B radiation

Besides acting as an UV-B radiation attenuator, flavonoids perform several other functions such as protection and defence against herbivory, insects and microbes⁶⁹, rhizospheric biological communication⁷⁰, polar auxin transport⁷¹, pollen fertility¹⁴, insect pollination through the production of colourful anthocyanin in petals, absorbing visible light spectra of different wavelengths⁷², and as an antioxidant to inhibit the production of ROS^{4,11}. They also have health-promoting effects such as cardioprotective, neuroprotective, anti-inflammatory, antioxidant, anticancer effects on humans and animals⁷³, and play a significant role in seed germination⁷⁴. Also flavonoids can serve as chemotaxonomic markers due to their variation between species and population⁷⁵. The functions of flavonoids in plants might be directly or indirectly controlled by UV-B radiation. Figure 4 depicts the overall influence of UV-B radiation on the functions of flavonoids in plants. Izaguirre *et al.*⁷⁶ found that the herbivory was compromised by UV-B radiation in *Nicotiana longiflora* and *Nicotiana attenuata* due to increase in level of flavonoids. Kuhlmann and Müller⁷⁷ found that

Table 1. Impact of UV-B radiation exposure on flavonoids content in different plants species

Plant	UV-B radiation dose/condition	Response of different flavonoids	Reference
<i>Astragalus membranaceus</i>	5.4–172.8 kJm ⁻² d ⁻¹ for 0.5–16 h	Under optimal elicitation dose (86.4 kJm ⁻² d ⁻¹), total isoflavonoids content increased by 2.29-fold against control	65
<i>Kalanchoe pinnata</i>	4–15 Wm ⁻² d ⁻¹ for 5 h	Quercetin content increased significantly	91
<i>Vaccinium corymbosum</i> L. cv. Brigitta and Bluegold	0.07, 0.12 and 0.19 Wm ⁻² d ⁻¹ for 6–74 h	Rutin content increased by 7.8% in Brigitta with 0.07 Wm ⁻² dose, whereas in Bluegold it decreased by 69% at the same dose. Among anthocyanidins, delphinidin was the most abundant and increased by 98% in Brigitta cultivar at a higher dose	45
<i>Vitis vinifera</i> cv. Tempranello	5.98 and 9.66 kJm ⁻² d ⁻¹ at two stages from fruit set to ripeness (FS) and onset of veraison to ripe (OV)	In berry skin malvidin 3-O-glucoside showed highest content and increased by 9.3% from FS with 5.98 kJm ⁻² dose. Among flavonols, myricetin 3-O-glucoside increased with both doses, but at 5.98 kJm ⁻² it increased by 33% and 46% from FS and OV respectively	90
<i>Glycine max</i> var. Dongnong, Yunhe and Nannong	5–40 μWcm ⁻² d ⁻¹ for 6 h during seed germination	Total isoflavone content in Dongnong, Yunhe and Nannong increased by 56%, 32%, 15% respectively, with 10 μWcm ⁻² dose, whereas no further increase was found at higher doses	92
<i>Ocimum basillicum</i>	2.30, 3.60 and 4.80 Wm ⁻² d ⁻¹ for 4–10 h at the post-harvest stage	At an intermediate (3.60 Wm ⁻²) dose, quercetin, kaempferol, rutin, catechin and luteolin contents increased by 0.41-, 0.65-, 0.68-, 0.85- and 1-fold respectively	66
<i>Capsicum annum</i> cv. Coronel	1.14 kJm ⁻² d ⁻¹ for 4 h over 7 and 14 days of experiment	Flavone apigenin was the major flavonoid, and 50% increase in apigenin 8-C-hexoside content was found over the 14-day experiment	93
<i>Lycopersicon esculentum</i> Mill var. Pusa rohini	5600 μWcm ⁻² d ⁻¹ for 20–60 min	Quercetin content was significantly increased by 5.19% with 60 min exposure	94
Grass species (<i>Deschampsia antarctica</i> , <i>D. borealis</i> , <i>Calamagrostis epigeios</i>) and Sedge sp. (<i>Carex arenaria</i>)	Elevated UV-B radiation dose: 2.5 kJm ⁻² d ⁻¹ in field and greenhouse conditions	Only <i>C. epigeios</i> showed significant increase by 3.9-fold in total flavonoids content compared to ambient UV-B radiation	58
<i>G. max</i>	18 μWcm ⁻² d ⁻¹ for 6 h	Concentration of isoflavones daidzin, glycitin, genistin and daidzein decreased by 4.5%, 8.6%, 1.1% and 11.4% respectively	95
<i>Suaeda maritima</i>	12.25 kJm ⁻² d ⁻¹ for 6 h	Anthocyanin content increased by 171.4% and flavonoids content increased by 129.8% after 9 days of experiment	96
<i>Lactuca sativa</i> var. capitata cv. Theodore RZ	0.11 kJm ⁻² d ⁻¹ for 5 days	Quercetin content increased tendentially and no significant changes were found in luteolin and anthocyanin	97
<i>Asparagus officinalis</i> cv. Gijnlim	0.54 and 1.08 kJm ⁻² d ⁻¹ for 2 and 22 h at post-harvest stage respectively	Quercetin-3,4'-O-diglucoside concentration was increased six-fold and two-fold compared to control in apical and basal spears respectively, after 22 h treatment	98
<i>Artemisia annua</i> L.	2.8 Wm ⁻² d ⁻¹ for 3 hr	Total flavonoid contents increased by 2.4 fold in UV-B radiation treated plants as compared to control	42

Brevicoryne brassicae, a cabbage aphid showed reduced performance on broccoli plants exposed to higher UV-B radiation (19 kJm⁻²d⁻¹). This might be because of stimulation of higher content of flavonoids that has been indirectly constraining reproduction of the aphid. In *Arabidopsis*, UV-B radiation increased flavonoids accumulation toward the radiated side of roots, that leads to decreased auxin transport and its distribution due to alteration in the abundance of auxin carrier AUX1 and PIN2 on the radiated side; ultimately asymmetric root growth occurs, resulting in root bending⁷⁸. In developing leaves

of barley, flavones such as saponarin and lutanarin increased under UV-B radiation as a strategy to decrease DNA and protein damage⁷⁹. Two isolines, viz. standard line (having moderate levels of flavonoids) and magenta line (having reduced levels of flavonoids) of the Clark cultivar of soybean revealed different sensitivity under UV-B radiation at the proteomic level⁸⁰. This suggests that high level of flavonoids in standard line of soybean causes reduction in sensitivity towards UV-B⁸⁰. Flavonoids also play a prominent role in the environment, such as interaction between plants and microbes. A reduced

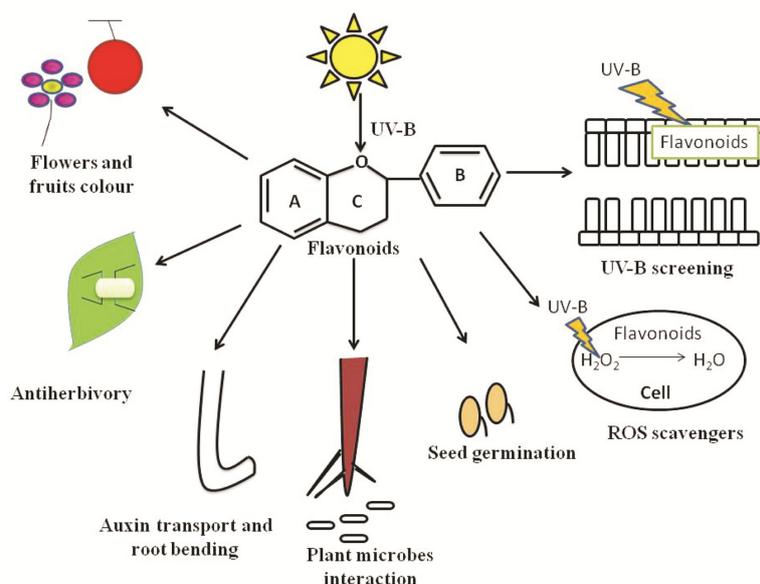


Figure 4. Different functions of flavonoids in plants under the influence of UV-B radiation.

arbuscular mycorrhizal (AM) fungus infection was found in *Calamagrostis epigeios* and *C. arenaria* under UV-B radiation⁸¹. High levels of UV-B radiation cause a decrease in arbuscules number in the host plant roots, arbuscules are accountable for the exchange of nutrients between the host plant and fungi. Van de Staaij *et al.*⁸¹ suggested that UV-B radiation influences AM association via differences in flavonoids content in above- and below-ground plant parts. In general, UV-B radiation enhanced the biosynthesis of polyphenolics like lignins, tannins that may restrict or decrease the microorganisms development including various fungal species. Accumulation of flavonoids in the roots could also affect the nodulation and symbiotic functions in elevated UV-B radiation exposed leguminous plants⁸². Choudhary *et al.*⁸³ reported that an enhancement in the flavonoids content might be responsible for decrease in the weight and number of root nodules in *V. radiata*. In addition, floral parts such as sepals, petals and ovaries have shown higher accumulation of flavonoids under UV-B radiation. Amongst the floral parts, ovary was found to be highly shielded from UV-B radiation than the others, which was attributed to the constitutively higher concentration of flavonoids^{84,85}. Several studies reported pollen as most sensitive reproductive tissue to UV-B radiation exposure⁸⁵⁻⁸⁷. It has been found that UV-B radiation-induced accumulation of flavonoids works as an important factor for the flower and fruit colour formation. In *Anigozanthos* species, UV-B radiation induce anthocyanin accumulation, which is primarily responsible for the bright and attractive colour of flowers^{85,88}. In *Malus* species, treatment of a pre-mature bud that breaks the UV-B radiation exposure affected the colouration of petals due to decreased biosynthesis of anthocyanidin, causing pink colouration of petals instead of the normal red colour^{85,89}. Further, changes in the colour

of petals may modulate attraction of pollinators towards the flowers and subsequently influence reproductive success of plants⁸⁵. Colour of fruits is also used as an indicator of their ripening, unpalatability or toxicity and mesmerize pollinators to eat the fruits and disperse the seeds therein⁸⁵. Ravagila *et al.*⁴⁸ revealed that flavonoids play an important role in fruit colour and flavour in nectarine and accumulation of these flavonoids might be further enhanced by exposure to UV-B radiation and white light. UV-B radiation also increased the concentration of extractable anthocyanin and colour density of the must of grape berry. Thus exposure of UV-B radiation might help to improve the quality of must for the production of wine⁹⁰.

Conclusions

Based on current evidences, it became clear that UV-B radiation is an important environmental stimulus that regulates biosynthesis of flavonoids at the transcriptional level of genes of the biosynthesis pathway, ultimately affecting accumulation of these flavonoids in plants. It is further regulated by appropriate dose, strength, time of exposure of radiation, developmental age, structure of flavonoids and several other environmental factors. The appropriate dose of UV-B radiation as an elicitor is important, as the high dose might also become a distress rather than eustress for accumulation of secondary metabolites. UV-B radiation also affects the functions performed by flavonoids in plants, by increasing or decreasing their contents in plant tissues. More studies are required involving medicinal and aromatic plants, trees, grasses and sedges to further strengthen the current state of knowledge, and improve the genetic and

transcriptomic regulation of secondary metabolites under exposure to UV-B radiation.

Future prospects

Besides performing several functions in plants, flavonoids are also a good source of health-promoting pharmaceutical products for humans. Although sufficient information is available for the regulatory role of UV-B radiation on flavonoids accumulation, advanced research in this area is required, especially by involvement of diverse plant groups. By improving the fundamental knowledge of UV-B radiation perception, signal transduction and subsequent regulation of transcription factors and genes of the biosynthesis pathway, the appropriate dose of UV-B radiation could be treated as a tool for enhancing flavonoid contents in plants for meeting its demand in pharmaceutical industry.

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